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ON NEW FACTS LATELY PRESENTED IN OPPOSITION TO THE HYPOTHESIS OF BIPOLARITY OF MARINE FAUNAS.

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BIPOLARITY in the distribution of marine animals, indicated by Théel as early as 1886, has been proposed as a theory by G. Pfeffer.[1] Later, J. Murray[2] accepted the theory and tried to support it by a careful collection of facts. From the beginning the present writer, chiefly relying on the investigation of the distribution of decapod crustaceans, vigorously objected to the theory, and expressed his views as early as 1894 and 1895,[3] contending that the cases introduced by Pfeffer were not correct. In 1896, after the publication of Murray's paper, the writer published an article[4] dealing with the subject more closely, and arrived at the conclusion that bipolarity does not exist as a general law of distribution among the decapod crustaceans, and that it seems very improbable that such a law may prevail among other groups of animals.

J. Murray disregarded these objections, and on different occasions[5] continued advancing bipolarity as a distributional fact, which called forth repeated objections on the part of the writer.[6] Since then (1897) other zoölogists have taken part in the discussion, and at present we possess the results of a number of investigations in special groups of animals, dealing with the relations of the Arctic and Antarctic faunas. All the results obtained tend to show that the original contention of the writer, derived from a study of the decapods, is fully supported by the facts found among other groups, so that the theory held by Pfeffer and Murray, that both polar faunas are more closely related to each other than to any of the intermediate ones, is without support. In fact, there have been added very few cases of bipolarity of genera to the single case established by the writer in 1895,[1] and one case of a bipolar species, discovered by Chun, is to be looked upon with some suspicion, for he himself suggests an explanation. All this points to the confirmation of the opinion of the writer, that, although some cases of bipolarity may exist, such cases are extremely rare, and may be explained in one of the ways indicated in his paper of 1896, while the greater part of each polar fauna consists of peculiar forms, which show no closer connection with each other than with forms found in tropical latitudes.

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[1] *Versuch über die erdgeschichtliche Entwicklung der jetzigen Verbreitungsverhältnisse unserer Thierwelt*, p. 38. Hamburg, 1891.

[2] *Trans. Roy. Soc. Edinburgh*, vol. xxxviii (1896), No. 2, p. 494.

[3] *Jenaische Denkschr.*, Bd. viii (1894), p. 76, and *Grundzüge der marinen Thiergeographie*, p. 52. (This latter book was issued in December, 1895, but bears the date 1896 on the title-page.)

[4] *Zool. Jahrb., Syst.*, Bd. ix (1896), pp. 571 *ff.*

[5] *Nature*, vol. lv (1897), No. 1430, p. 500, and in *The Geograph. Journ.*, vol. xii (1898), No. 2.

[6] *Zool. Jahrb., Syst.*, Bd. x (1897), p. 217, and *Science*, vol. viii (1898), p. 516. Pfeffer (*Zool. Anzeig.*, Bd. xx, September, 1897) has referred to the first of these objections; but since he does not discuss the matter at all, and only doubts the ability of the writer to investigate this topic, it is better not to consider this note.

We will now review the chief results of the papers recently published, and then draw conclusions as to the theory of bipolarity. However, it is well to observe that some of the authors referred to did not give all the necessary data. Especially is there a lack of information as to the distribution of genera found in both polar seas, outside of their polar range. The writer has tried to supply this deficiency by consulting other papers, but as he cannot claim to be a specialist in the respective groups, he has in some cases failed. Further, a misunderstanding seems to exist on the part of some authors as regards the term "bipolarity"; they sometimes call a species or genus that is found in both polar areas bipolar, although it is also present in intermediate localities. But "bipolarity," as understood by Pfeffer and Murray and the present writer, implies that a bipolar form is wanting in the intermediate tropical parts of the seas, and the chief difficulty in the discussion is the explanation of such cases of *discontinuity* in distribution.

The first paper to be discussed is an investigation of the pelagic faunas of the Arctic and Antarctic, by C. Chun.[1] He collects the records of the occurrence of the animals constituting the plankton of the polar regions (Protozoa, Medusæ, worms, crustaceans, mollusks, Tunicata, and fishes), and although he complains in many cases of a general lack of information, especially as to the Antarctic pelagic life, he reaches some very important conclusions. He recognizes a general similarity of both faunas, which finds its chief expression in the prevalence of certain groups in both areas and the absence of others; and, further, he mentions the presence in both polar seas of two identical species, one a worm (*Sagitta hamata*), the other a Tunicata (*Fritillaria borealis*). The first case, that of *Sagitta hamata*, is treated more in detail, and Chun shows (after Steinhaus and Lohmann) that this species, which has been found near the surface in both polar seas, crosses the Atlantic Ocean. It is not, however, found there near the surface, but at considerable depths (300–1500 m.). Thus, for this pelagic species, a connection of the Arctic and Antarctic range through the tropics, but in deeper water, is established (analogous to the connection of littoral polar forms along the bottom of the deep sea), and Chun concludes that this connection, once having been proved, is sufficient to explain other cases, and that there is no need to have recourse to theories which, like Pfeffer's and Murray's, go back to former climatic conditions of the earth. Yet in the writer's opinion this conclusion is not satisfactory. We do not want to know how an individual case *may* be explained, but we want to know how it can be explained *correctly*. Although we must appreciate the value of the case represented by *Sagitta hamata*, still there remains the question to be settled, whether other cases of bipolarity, which may be discovered, are really cases of bipolarity, where there is no connection of both ranges, and whether such cases are to be explained by the Pfeffer-Murray theory, or by other means, as indicated by the present writer. But at any rate Chun's paper shows plainly that cases of bipolarity among pelagic organisms seem to be *very rare*.

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[1] *Proc. Acad. Philad.* (1895), pp. 189–197.

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[1] *Die Beziehungen zwischen dem arktischen und antarktischen Plankton.* Stuttgart, 1897.

All the other papers under consideration discuss littoral and abyssal animals. In an article on the history of the marine fauna of Patagonia, H. von Ihering[1] compares the Antarctic mollusks with those of the Arctic. He mentions 9 species that are found in both polar seas, but at the same time he says that this list comprises almost exclusively such species as are of a very large or universal distribution. The connection of the polar localities of these forms is chiefly through the deep sea. There are no true bipolar *species*, and if we regard the *genera* present or wanting in the Arctic and Antarctic molluscan faunas, both differ considerably.

Breitfuss[2] has published a study of the distribution of the calcareous sponges of the Arctic seas, and incidentally compares them with those of the Antarctic. Of 42 Arctic species only a few (6) cross the equator, and a single one extends its range into the southern polar regions (*Grantia capillosa*). The rich Calcispongiæ fauna of the Australian and New Zealand coasts is very distinct from that of the Arctic, and from the Magellan, South Georgian, and Kerguelen regions only 6 species (belonging to 4 genera) are known, which, with the exception of *Grantia capillosa*, are different from the northern species; and of these genera one (Leucetta) is missing in the Arctic Ocean, while, on the other hand, numerous Arctic genera (6 out of 11) are not known from the Antarctic. No case of bipolarity, either of a species or genus, is mentioned, and the author says nothing about a resemblance of faunas of both seas.

Herdman[3] refers to the extra-tropical southern tunicate fauna of Australia, and, without going into further detail, states that there is no special relationship between it and the tunicate fauna of the northern hemisphere. As to Murray's extracts, from his report on the distribution of the Challenger-Tunicata, he says that the distributional data given in this report are not complete, and, he says, "have to be added to or modified in such a way as to entirely change the nature of their evidence, and show that there is no such close resemblance between the northern and southern polar faunas as Dr. Murray and others have supposed." In fact, he states plainly that among the simple ascidians no cases of bipolarity are known.

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[1] Zur Geschichte der marinen Fauna von Patagonien, *Zool. Anzeig.*, Bd. xxvii, December, 1897.

[2] Die arctische Kalkschwammfauna, *Arch. f. Naturg.*, Bd. i (1898), Heft 3.

[3] *Ann. Mag. Nat. Hist.*, Ser. 7, vol. i (1898), and *Trans. Liverpool Biol. Soc.*, vol. xii (1898), p. 251.

D'Arcy W. Thompson[1] has reëxamined the list of bipolar animals given by J. Murray. This list contains nearly 100 species, but d'Arcy W. Thompson shows (p. 347) that there are among them "more than one-third in which grave doubt as to their identification was expressed by the original describers, or in which the identification has been doubted or denied by later writers. In somewhat more than another third the evidence of identity is inconclusive or even inadmissible by reason of the nature of the examination to which the specimens were subjected, or by reason of the small size of the objects and lack of adequate marks of characterization. Of the remaining forms, about a dozen find their northern representatives in the Japanese seas, where they form part of a fauna predominantly southern in its relations, and where at least the occurrence of any particular form cannot be taken, *ipso facto*, as evidence of a boreal center of distribution."

After deducting these forms the list shrinks into very little. There remains, aside from 12 deep-sea species, only a single littoral annelid species (*Terrebellides strœmii*), and 2 pelagic species, a mollusk, *Janthina rotundata*, and a copepod, *Calanus finmarchicus;* but even these last two hardly seem to be bipolar, since neither of them is recorded from further south than 35° S. L., and the latter seems to be rather a cosmopolitan form (see note on p. 349, *loc. cit.*).

Further, d'Arcy W. Thompson gives an examination of the Antarctic fishes, isopods, and amphipods, with special reference to bipolarity. He finds no species in any of these groups to inhabit both the Arctic and Antarctic Oceans, and he sees no signs of a likeness of both faunas.

A valuable series of monographs has been published by

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[1] On a Supposed Resemblance between the Marine Faunas of the Arctic and Antarctic Regions, *Proc. Roy. Soc. Edinburgh* (1898), pp. 311–349.

H. Ludwig,[1] treating of the distribution of the holothurioids, crinoids, and ophiuroids, with special reference to their polar ranges. The part on the holothurians is especially interesting, since it was this group that first suggested to Théel the idea of bipolarity. According to Ludwig there are no bipolar species, and, in respect to the genera, there is not a single instance that shows the slightest indications of bipolarity. Out of 10 genera found in both polar regions, 5 (Stichopus, Cucumaria, Thyone, Phyllophorus, Chirodota) have been found abundantly in the littoral parts of the tropics, and 4 (Bathyplotes, Mesothuria, Trochostoma, Ankyroderma) are connected in the deep sea; and the same seems to be true of Psolus, which has been reported from tropical latitudes, although it seems to be rarer there. Aside from these 10 genera mentioned, there are 9 genera peculiar to the Antarctic, and 6 peculiar to the Arctic (but some of them extend into the tropics), thus giving a different character to the two faunas. The general result in the other two groups studied by Ludwig is practically the same; there are no bipolar species, and the number of genera peculiar to each fauna is larger than the number of genera common to both. Among the crinoids there is only 1 genus (Antedon) found in both areas, while 3 are peculiar to the Antarctic (2 of them abyssal) and 1 peculiar to the Arctic, and among the ophiuroids 6 genera are common to both areas, while 9 are peculiar to the Antarctic and 8 to the Arctic.

The genus Antedon found in both polar seas is very interesting. Both the Antarctic and Arctic species belong exclusively to two sections of the genus, *A. eschrichti* and *A. tenella*. The Tenella group is found in all parts of the world, so that there is nothing remarkable about its distribution. The Eschrichti group, however, contains 4 littoral Antarctic species and 3 littoral Arctic species (2 of them also abyssal), the latter all from the North Atlantic. Now it is very significant that some kind of a connection is afforded by one of the Antarctic species, namely, *A. rhomboidea*. This species has been found in the littoral of the southern end of America, and its range extends northward along the western coast of America to 22° N. L., but there it has been dredged at greater depths (1200–1400 m.). Although no species of this group has yet been found in the northern Pacific, it is very probable, nevertheless, that such species do exist. In that case we would here have again an instance of a connection, along the western coast of America, of an apparently bipolar group of marine animals. Examples of this kind have been pointed out, by the present writer, among the decapods.

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[1] *Hamburger Magalhaensische Sammelreise.* Holothurien, 1898; Crinoideen, 1899; Ophiuroideen, 1899.

Of the 6 ophiuroid genera common to both the polar seas, 4 (Ophioglypha, Ophiactis, Amphiura, Ophiacantha) are also represented in the littoral of the tropics. The 2 remaining genera (Ophiocten, Gorgonocephalus) are chiefly abyssal genera, and, as far as the writer could determine, Ludwig does not give any information — at least, Ophiocten is also found in tropical latitudes.

Thus in these three groups we have again the same result: that bipolarity, if present at all, is extremely rare, and that the most prominent feature of the respective faunas of the polar seas consists in their dissimilarity.

Yet Ludwig calls attention to a certain general likeness of both faunas, expressed by the mutual prevalence of certain genera and the mutual lack of others as compared with the tropic faunas. This is not to be regarded at all as a remarkable fact, and has no connection with the question under discussion; indeed, it would be very strange if other conditions prevailed. When, out of a number of genera present in the tropics, a certain number disappears as we approach either pole, while a certain number does not, this shows only that the latter are not affected by the change of conditions, — chiefly climatic, — while the former are, and of course by the disappearance of a number of types the percentage of the remaining must increase, if the deficiency is not made up by other genera making their appearance in the colder regions. This is again an instance where statistics give a wrong idea of the true conditions; the increase of the percentage of certain genera in the polar seas is not due to an actual increase of species and a more vigorous development, but only to the lack of species of other genera.

Lastly, we have a paper, by O. Buerger,[1] treating of a group of worms, the nemertines. Buerger does not go much into detail, but we must attribute this chiefly to our scant knowledge of this group. Again, there are no bipolar species; the only two species which have been found in corresponding latitudes on both hemispheres are circum-tropical, and enter extra-tropical parts only on the northern and southern limits of their range. As regards the genera, all Antarctic genera (9) are also found in the Arctic. Buerger says that a general similarity of both polar faunas is thus indicated, but the lack of 12 Arctic genera in the Antarctic does not support this view; and since he says, further, that neither of the faunas seems to possess very characteristic types, as do the tropics, it is evident that these 9 genera common to both polar faunas are also represented in the tropics. There is, however, one genus that seems to be bipolar; Carinoma, which has been found on the coast of England (*C. armandi*) and in the Straits of Magellan (*C. patagonica*).

There is no doubt that the facts presented here do not at all support the theory of bipolarity. The contention of Pfeffer and Murray is that bipolarity forms a very striking feature of the polar faunas. This has been denied by the present writer with regard to the decapod crustaceans, and now von Ihering has confirmed this latter opinion for the mollusks, Breitfuss for the Calcispongiæ, Herdman for the tunicates, d'Arcy W. Thompson for the fishes, isopods, and amphipods, Ludwig for the holothurians, crinoids, and ophiuroids, Buerger for the nemertines, and Chun for the entire bulk of the pelagic fauna.

Two cases of bipolarity of species and one of genera have been discovered, and when we add these to the single case previously established (Crangon), we have altogether four cases of true bipolarity which are to be explained by a theory. In all other cases the supposed bipolar range of a species or group has been connected by intermediate localities, and these connections are of two kinds: (1) connection along the bottom of the deep sea or in deeper strata of the tropical parts of the open sea (Ortmann, von Ihering, Thompson, Chun, Ludwig); (2) connection along the western shores of the continents, mostly connected with a descending of the respective forms into deeper water (Ortmann, Bouvier, Thompson, Ludwig).

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[1] *Hamburger Magalhaensische Sammelreise.* Nemertinen, 1899.

It is possible that by these ways cases of true bipolarity may develop, provided these connections become discontinued. The writer has explained a true case of bipolarity (Crangon) by one of these ways. But, on the other hand, it is also possible that bipolarity is to be explained by the Pfeffer-Murray theory in some cases by former conditions of the earth's history, especially those existing at the beginning of the Tertiary period. Yet we do not know any concrete case of this kind, and we must wait for further investigation to show whether bipolarity as a *relic* of older times is realized in the geographical distribution of any marine animals.